

ANTHROPOLOGY

Symbolic use of marine shells and mineral pigments by Iberian Neandertals 115,000 years ago

Dirk L. Hoffmann,^{1*} Diego E. Angelucci,² Valentín Villaverde,³ Josefina Zapata,⁴ João Zilhão^{5,6,7*}

Cueva de los Aviones (southeast Spain) is a site of the Neandertal-associated Middle Paleolithic of Europe. It has yielded ochred and perforated marine shells, red and yellow colorants, and shell containers that feature residues of complex pigmentary mixtures. Similar finds from the Middle Stone Age of South Africa have been widely accepted as archaeological proxies for symbolic behavior. U-series dating of the flowstone capping the Cueva de los Aviones deposit shows that the symbolic finds made therein are 115,000 to 120,000 years old and predate the earliest known comparable evidence associated with modern humans by 20,000 to 40,000 years. Given our findings, it is possible that the roots of symbolic material culture may be found among the common ancestor of Neandertals and modern humans, more than half-a-million years ago.

INTRODUCTION

The emergence of symbolic material culture represents a threshold in the evolution of our species. Artifacts with a functional value that lies in the informational realm are proxies for the presence of language and, thus, of the fundamental aspects of human cognition as we know it (1, 2). For more than a century, the evidence seemed to suggest that symbolic artifacts appeared relatively late in the Pleistocene and in the context of the so-called Upper Paleolithic revolution—the apparently sudden appearance in Europe, around 40 thousand years (ka) ago, of cave art, sculpted figures, decorated bone tools, and jewelry made of bone, tooth, ivory, shell, or stone (3, 4).

The past two decades of research have critically shaken the empirical foundations of this paradigm. In both southern and northern Africa, perforated and ochred marine shell beads were retrieved in a number of sites of the Middle Stone Age (MSA) dated to the Last Interglacial, more than 70 ka ago (5–7). These discoveries led to suggestions that such material symbols represented “modern behavior,” the emergence of which being understood (i) as part and parcel of the speciation of anatomically modern humans and (ii) as an explanation of the latter’s eventual prevalence over coeval Eurasian humans. Being anatomically archaic, such Eurasian populations, namely, the Neandertals, were thereby assumed to have also been behaviorally archaic, that is, devoid of symbolism and possibly even of language (8, 9).

On the basis of the association of Neandertals with tooth and bone pendants in the Châtelperronian culture of southwestern Europe, an alternative view was that symbolic material culture appeared as the result of a complexification of social relations—triggered by demographic growth, requiring the production of modes of individual and group identification, and occurring across the entire Old World, irrespective of human taxonomic boundaries (10, 11). This alternative was furthered by the presence of perforated and ochred marine shells, yellow and

red colorants, and shell containers with residues of complex pigment mixes—the same kinds of finds made in the African MSA—in the Neandertal-associated Middle Paleolithic of Cueva de los Aviones (Cartagena, Region of Murcia, Spain; 37°35′7.30″N, 0°59′8.66″W) (Figs. 1 to 3) (12). Radiocarbon dating of food shells (*Patella ferruginea* limpets) dated this archaeological context to a period 45 to 50 ka ago, slightly earlier than the Châtelperronian but still within the range of some age estimates for the first wave of modern human dispersals into Europe that would eventually lead to Neandertal demise (13). Therefore, it remained possible that the finds from both Aviones and the Châtelperronian could have been associated with modern humans, either directly, as its makers, or indirectly, as providers of models copied by Neandertals in acculturation or in an “imitation without understanding” manner (14–16).

RESULTS AND DISCUSSION

Cueva de los Aviones is a sea cave. The base of its fill, found at sea level, is a cemented marine conglomerate—the beach rock of a Last Interglacial sea-level high stand (12). Elsewhere in the Mediterranean, deposits of this age are found 4 to 7 m above present sea level, but this stretch of the Spanish Mediterranean coast is an area of relative subsidence (17). Analysis of these deposits has posed several challenges. First, the overlying archaeological breccia is contiguous with the basal conglomerate and itself features no significant internal discontinuity. Second, the age estimates obtained through radiocarbon dating are at the limits of detection for this method. Third, shell can behave in an open-system manner, leading sometimes to radiocarbon results spanning the later Pleistocene and the Holocene for samples that are known with certainty to be of much earlier age (18). Finally, the deposit’s abundant shellfish remains suggest close proximity to the sea, whereas a marine isotope stage (MIS) 3 chronology implies a distance of 1 to 2 km from the paleoshoreline. For these reasons, it was necessary to verify that the radiocarbon dates obtained were not just minimum ages.

To do so, we sampled the flowstone capping the deposit (Fig. 2). Its stratigraphic relationship with the underlying sediment is demonstrated by (i) the 1985 excavation’s notes and stratigraphic records (19) and (ii) field observation, supported by the comparison between photos taken before and after the excavation with those made when the extant section was geologically described and sampled, in 2009 and 2013 (Figs. 1, C and D, 2A, and 4 and figs. S2 to S4). Lying conformably and in continuity with the underlying sediments, as is well apparent

¹Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany. ²Dipartimento di Lettere e Filosofia, Università degli Studi di Trento, via Tommaso Gar 14, 38122 Trento, Italy. ³Departament de Prehistòria i d’Arqueologia, Universitat de València, Av. Blasco Ibañez 28, 46010 València, Spain. ⁴Àrea de Antropologia Física, Facultat de Biologia, Universitat de Murcia, Campus Universitario de Espinardo, 30100 Murcia, Spain. ⁵Departament d’Història i Arqueologia (Seminari d’Estudis i Recerques Prehistòriques), University of Barcelona, c/ Montalegre 6, 08001 Barcelona, Spain. ⁶Institució Catalana de Recerca i Estudis Avançats (ICREA), Passeig Lluís Companys 23, 08010 Barcelona, Spain. ⁷Centro de Arqueologia da Universidade de Lisboa (UNIARQ), Faculdade de Letras, Campo Grande, 1600-214 Lisboa, Portugal.

*Corresponding author. Email: dirk.hoffmann@eva.mpg.de (D.L.H.); joao.zilhao@ub.edu (J. Zilhão)

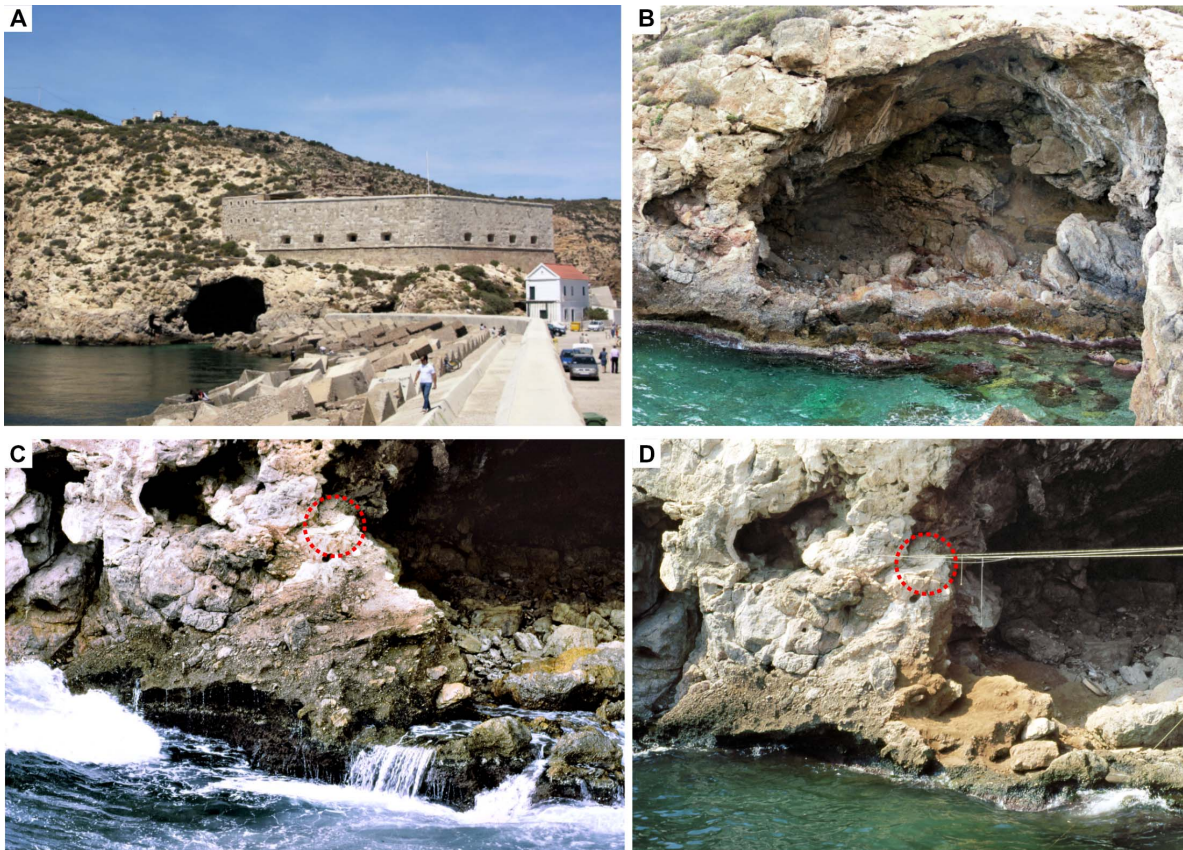


Fig. 1. Site setting. (A) The site seen from a breakwater in the Cartagena harbor. (B) Overview of the cave. Brecciated Pleistocene remnant before (C) and after (D) its 1985 excavation. The dotted circles in (C) and (D) indicate the position of the dated flowstone, clearly overlying the excavated deposit.

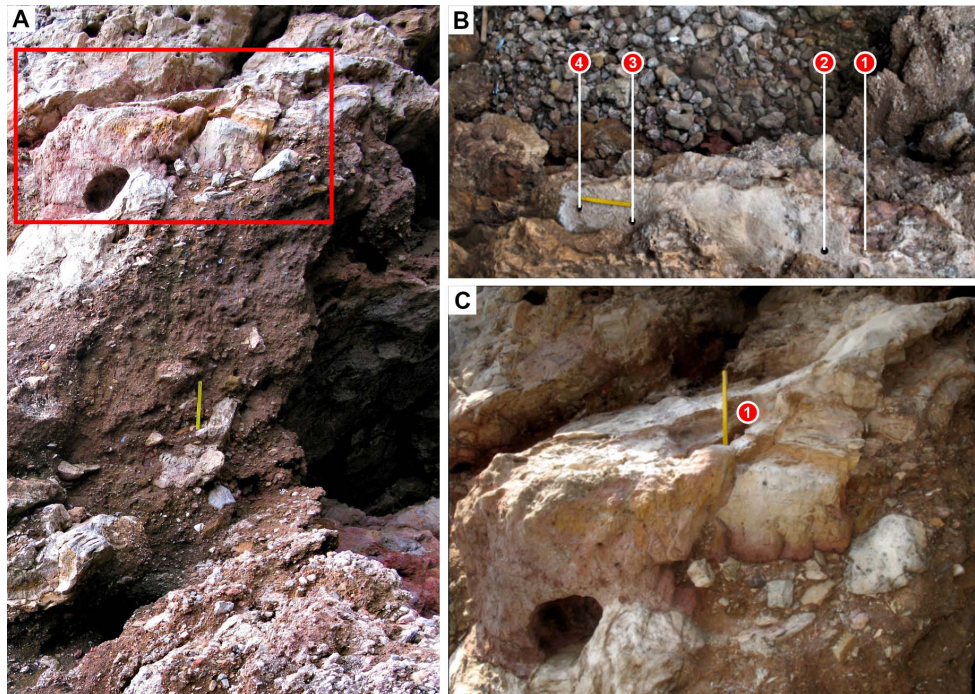


Fig. 2. Sampling. (A) Extant stratigraphic section. Zenithal (B) and frontal (C) views of the flowstone capping the excavated deposit. The rectangle in (A) denotes the area enlarged in (C). A 20-cm yellow ruler was used for scale in (B) and (C), in which the numbers denote the samples taken.

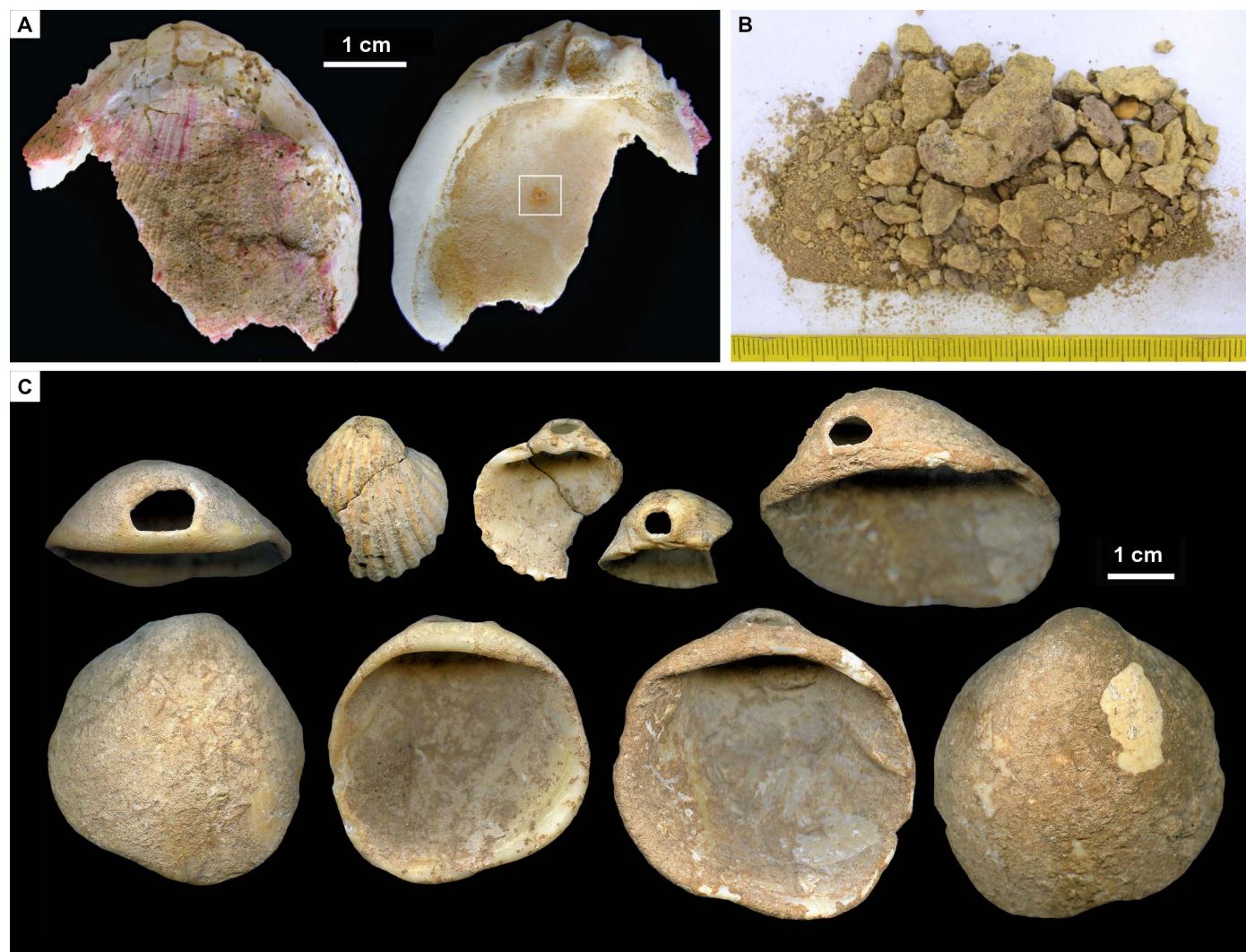


Fig. 3. Symbolic finds [after Zilhão et al. (12)]. (A) *Spondylus* shell with remnants (indicated by the white square) of a pigmentary compound mixing ground inclusions of hematite and pyrite in a red lepidocrocite basis. (B) Large lump of natrojarosite, a mineral whose only known archaeological use is in cosmetics. (C) Perforated *Acanthocardia* and *Glycymeris* shells (red hematite residues were found adhering to the inner side of the larger *Glycymeris*).

in our sectioned samples, the time of deposition of this flowstone therefore provides an unambiguous minimum age for the Cueva de los Aviones symbolic finds. In addition, note that, despite >25 years of exposure to weathering, the 1985 section remained intact, owing to its heavy cementation, which explains the preservation in this part of the site of a remnant of the original fill, now >90% lost, and confirms the stratigraphic integrity of the archaeological context.

To determine the time of formation of the flowstone, we applied the U-Th method to four samples. Sample 1 was cut from the extant vertical section, and samples 2 to 4 were cored from above (Fig. 2, B and C, and the Supplementary Materials). U-Th measurements were undertaken on subsamples taken from near the base of each sample. For samples 1 and 3, which cover the entire thickness of the flowstone and reach the flowstone-sediment boundary, we find consistent results of 117 ± 3 ka and 115 ± 1 ka (table S1 and the Supplementary Materials). These results prove that flowstone had already begun to form atop the Aviones archaeological deposit by 114 ka ago, the youngest possible age of the two results. Global records and the submerged Mallorca speleothems show

that sea level began to drop from the last of the high stands of MIS 5e around 120 ka ago (20, 21) and dropped significantly around 118 ka ago (22). Taking 120 to 118 ka as the time when, once the sea had retreated, continental sediments could start accumulating inside the cave, above the beach rock, we can conclude that the deposit represented by the Cueva de los Aviones remnant accumulated quite rapidly during a period of no more than about five millennia.

The ages available for the sites of the African MSA that yielded comparable finds have all been obtained by luminescence dating and therefore typically have associated 2σ uncertainties of at least 6%. This situation hinders comparison with the U-series chronology for Cueva de los Aviones, which is based on results that are about six times more precise. In addition, significant disagreement between estimates derived by different research groups for the same African sites or cultures persists (23, 24). Nevertheless, the most recent luminescence-derived estimates for the Still Bay culture of South Africa, to which the ochred shell beads from Blombos Cave belong and which is the earliest unambiguously defined South African context with symbolic artifacts, suggest

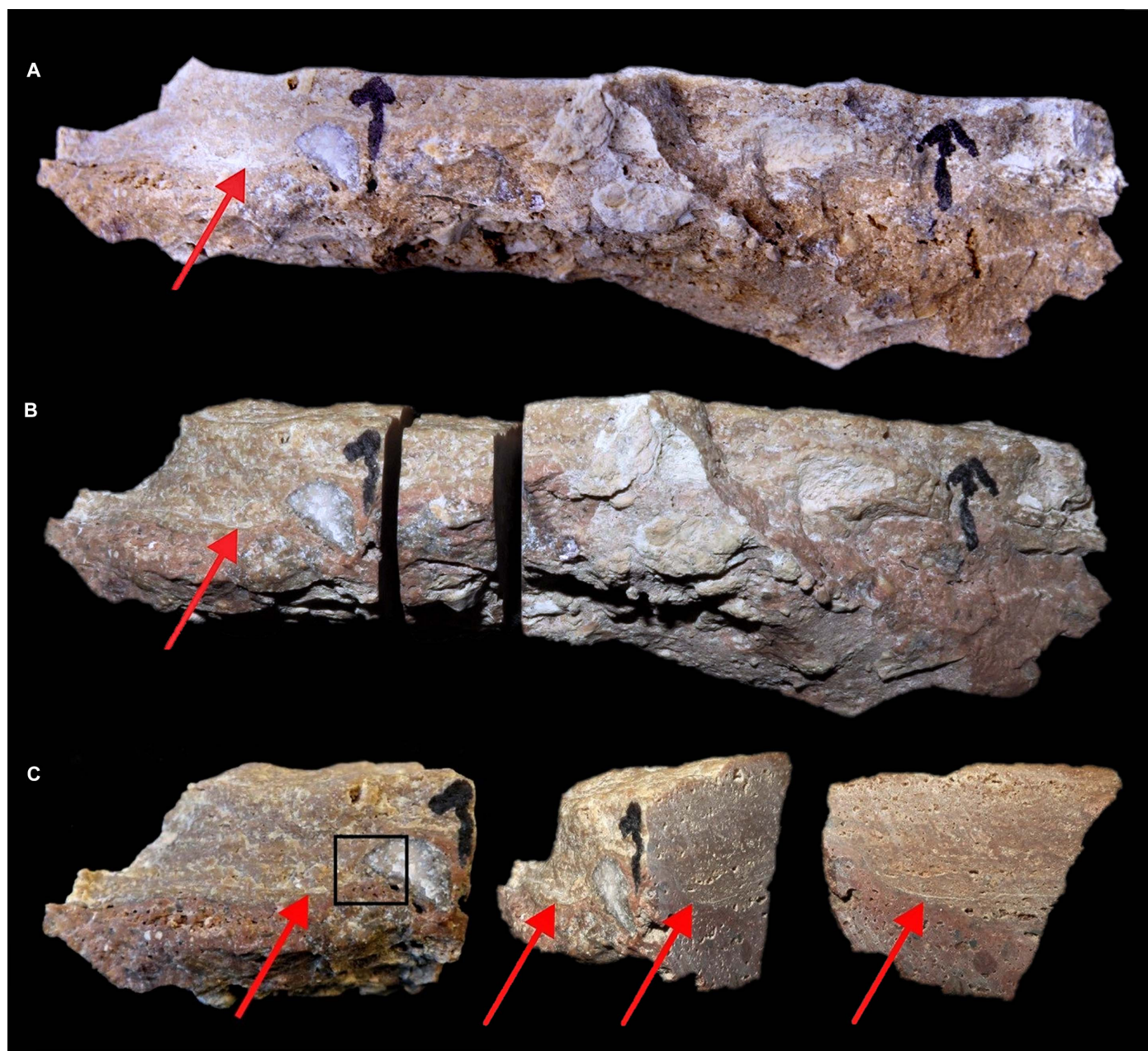


Fig. 4. Sample AVI 13-1c. (A) Sample piece AVI 13-1c after removal from flowstone section LS01 (12) at the interface between the flowstone and the underlying cemented sediment LS02 (figs. S2 and S4). Note the cemented sediment of the LS02 unit adhering to the bottom part of the sample. (B) Sample piece AVI 13-1c after cutting out a section for U-series subsampling (fig. S7D). (C) Piece on the left in (B) viewed from different angles. The red arrows indicate the boundary between the LS01 flowstone and the LS02 cemented sediment. The black square indicates where flowstone formed around a sediment particle.

that this culture began 78.7 ka ago, at the earliest (25). The age estimated for the shell bead horizon at Grotte des Pigeons, Morocco, is, within error, the same (82.5 ± 5.3 ka ago) (7), as is the mean age estimate (around 92.5 ka ago) for the Middle Paleolithic of Qafzeh Cave, in Israel, which yielded colorants as well as perforated and ochred *Glycymeris* shells identical to those from Cueva de los Aviones, but in a modern human-associated context (26–28).

The Neandertal-associated evidence from Cueva de los Aviones therefore substantially predates, by 20 to 40 ka, anything comparable known in Africa or western Asia to date. In conjunction with the evidence that cave painting in Europe dates back to at least 64.8 ka ago

(29), it leaves no doubt that Neandertals shared symbolic thinking with early modern humans and that, as far as we can infer from material culture, Neandertals and early modern humans were cognitively indistinguishable.

The auditory structures of the Atapuerca/Sima de los Huesos fossils show the ability to produce and perceive the sounds emitted during modern human spoken language (30); and the time spans involved in the evolution of the neural hardware required for that ability to evolve (1) support an ancient origin for language, which is symbolic by definition. Whatever one thinks about the place of Neandertals in human taxonomic schemes, the corollary of these findings is that the capacity

for symbolism must have been inherited from a common ancestor. As a working hypothesis, we suggest that the origins of language and the advanced cognition characteristic of extant humans may precede the period before the divergence of the Neanderthal lineage, more than half-a-million years ago.

MATERIALS AND METHODS

Samples were collected from a flowstone section [LS01; (12)] capping the archaeological sections excavated in Cueva de los Aviones. One piece was removed with a hammer and a chisel, and three additional samples were core-drilled. Subsamples for U-Th dating were cut from the collected specimen using a band saw fitted with a diamond-coated cutting band. The CaCO_3 pieces were cleaned in an ultrasound bath and dried. Procedures for isotope dilution and purification followed the protocol outlined by Hoffmann *et al.* (31). Purified U and Th fractions were analyzed in 0.5 M HCl solution by multi-collector inductively coupled plasma mass spectrometry (MC-ICPMS). Analytical protocols for MC-ICPMS and data reduction are presented in detail by Hoffmann *et al.* (29, 32). More details about the samples and sample preparation presented in this study can be found in the Supplementary Materials. All U-series results are reported in table S1.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/2/eaar5255/DC1>

Supplementary Materials and Methods
Supplementary Text

fig. S1. Map of the Iberian Peninsula.

fig. S2. Cueva de los Aviones.

fig. S3. Stratigraphic position of the LS01 flowstone.

fig. S4. Sample AVI 13-1.

fig. S5. Flowstone pieces AVI 13-1a, AVI 13-1b, and AVI 13c.

fig. S6. Flowstone section LS01 (12) with position of drill cores AVI 13-2, AVI 13-3, and AVI 13-4.

fig. S7. Flowstone sample AVI 13-1.

fig. S8. Cross sections of drill core samples AVI 13-2, AVI 13-3, and AVI 13-4.

fig. S9. Osmond type isochron diagrams for sample AVI 13-1c.

fig. S10. Osmond type isochron diagrams for samples AVI 13-2, AVI 13-3, and AVI 13-4.

fig. S11. Dating results for five individual samples taken from the thin carbonate layer AVI 13-1b, showing uncorrected and corrected results.

fig. S12. Distance-age results for flowstone piece AVI 13-1.

fig. S13. Basal ages for samples AVI 13-1, AVI 13-2, AVI 13-3, and AVI 13-4.

table S1. U-series results for AVI 13-1, AVI 13-2, AVI 13-3, and AVI 13-4.

References (33–38)

REFERENCES AND NOTES

1. T. Deacon, *The Symbolic Species: The Co-evolution of Language and the Brain* (W. W. Norton and Company, 1997).
2. C. S. Henshilwood, F. d'Errico, *Homo Symbolicus: The Dawn of Language, Imagination and Spirituality* (John Benjamins Publishing Company, 2011).
3. R. White, Rethinking the Middle/Upper Paleolithic Transition. *Curr. Anthropol.* **23**, 169–192 (1982).
4. A. Gilman, Explaining the Upper Palaeolithic revolution, in *Marxist Perspectives in Archaeology*, M. Spriggs, Ed. (Cambridge Univ. Press, 1984), pp. 115–126.
5. C. S. Henshilwood, F. d'Errico, R. Yates, Z. Jacobs, C. Tribolo, G. A. T. Duller, N. Mercier, J. C. Sealy, H. Valladas, I. Watts, A. G. Wintle, Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science* **295**, 1278–1280 (2002).
6. C. Henshilwood, F. d'Errico, M. Vanhaeren, K. van Niekerk, Z. Jacobs, Middle Stone Age shell beads from South Africa. *Science* **304**, 404 (2004).
7. A. Bouzouggar, N. Barton, M. Vanhaeren, F. d'Errico, S. Collcutt, T. Higham, E. Hodge, S. Parfitt, E. Rhodes, J.-L. Schwenninger, C. Stringer, E. Turner, S. Ward, A. Moutmir, A. Stambouli, 82,000-year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 9964–9969 (2007).
8. C. S. Henshilwood, C. W. Marean, The origin of modern human behavior: Critique of the models and their test implications. *Curr. Anthropol.* **44**, 627–651 (2003).
9. R. G. Klein, Paleoanthropology. Whither the Neanderthals? *Science* **299**, 1525–1527 (2003).
10. F. d'Errico, The invisible frontier. A multiple species model for the origin of behavioral modernity. *Evol. Anthropol.* **12**, 188–202 (2003).
11. J. Zilhão, The emergence of ornaments and art: An archaeological perspective on the origins of “behavioural modernity”. *J. Archaeol. Res.* **15**, 1–54 (2007).
12. J. Zilhão, D. E. Angelucci, E. Badal-García, F. d'Errico, F. Daniel, L. Dayet, K. Douka, T. F. G. Higham, M. J. Martínez-Sánchez, R. Montes-Bernárdez, S. Murcia-Mascarós, C. Páez-Sirvent, C. Roldán-García, M. Vanhaeren, V. Villaverde, R. Wood, J. Zapata, Symbolic use of marine shells and mineral pigments by Iberian Neanderthals. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 1023–1028 (2010).
13. T. Higham, K. Douka, R. Wood, C. B. Ramsey, F. Brock, L. Basell, M. Camps, A. Arrizabalaga, J. Baena, C. Barroso-Ruiz, C. Bergman, C. Boitard, P. Boscato, M. Caparrós, N. J. Conard, C. Draily, A. Froment, B. Galván, P. Gambassini, A. García-Moreno, S. Grimaldi, P. Haesaerts, B. Holt, M.-J. Iriarte-Chiapusso, A. Jelinek, J. F. Jordá Pardo, J.-M. Maillou-Fernández, A. Marom, J. Maroto, M. Menéndez, L. Metz, E. Morin, A. Moroni, F. Negrino, E. Panagopoulou, M. Peresani, S. Pirson, M. de la Rasilla, J. Riel-Salvatore, A. Ronchitelli, D. Santamaria, P. Semal, L. Slimak, J. Soler, N. Soler, A. Villaluenga, R. Pinhasi, R. Jacobi, The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature* **512**, 306–309 (2014).
14. J.-J. Hublin, The modern human colonization of western Eurasia: When and where? *Quat. Sci. Rev.* **118**, 194–210 (2015).
15. C. Stringer, C. Gamble, *In Search of the Neanderthals* (Thames and Hudson, 1993).
16. P. Mellars, Neanderthal symbolism and ornament manufacture: The bursting of a bubble? *Proc. Natl. Acad. Sci. U.S.A.* **107**, 20147–20148 (2010).
17. T. Bardaji, A. Cabero, J. Lario, C. Zazo, P. G. Silva, J. L. Goy, C. J. Dabrio, Coseismic vs. climatic factors in the record of relative sea level changes: An example from the Last Interglacials in SE Spain. *Quat. Sci. Rev.* **113**, 60–77 (2015).
18. F. S. Busschers, F. Wesselingh, R. H. Kars, M. Versluijs-Helder, J. Wallinga, J. H. A. Bosch, J. Timmer, K. G. J. Nierop, T. Meijer, F. P. M. Bunnik, H. De Wolf, Radiocarbon dating of Late Pleistocene marine shells from the Southern North Sea. *Radiocarbon* **56**, 1151–1166 (2014).
19. R. Montes, La Cueva de los Aviones. Un yacimiento del Paleolítico Medio (Cartagena, Spain). *Memorias de Arqueología de la Región de Murcia* **2**, 35–38 (1991).
20. N. J. Shackleton, The 100,000-year ice-age cycle identified and found to lag temperature, carbon dioxide, and orbital eccentricity. *Science* **289**, 1897–1902 (2000).
21. J. A. Dorale, B. P. Onac, J. J. Fornós, J. Ginés, A. Ginés, P. Tuccimei, D. W. Peate, Sea-level highstand 81,000 years ago in Mallorca. *Science* **327**, 860–863 (2010).
22. G. E. Moseley, P. L. Smart, D. A. Richards, D. L. Hoffmann, Speleothem constraints on marine isotope stage (MIS) 5 relative sea levels, Yucatan Peninsula, Mexico. *J. Quat. Sci.* **28**, 293–300 (2013).
23. Z. Jacobs, R. G. Roberts, R. F. Galbraith, H. J. Deacon, R. Grün, A. Mackay, P. Mitchell, R. Vogelsang, L. Wadley, Ages for the Middle Stone Age of southern Africa: Implications for human behavior and dispersal. *Science* **322**, 733–735 (2008).
24. G. Guérin, A. S. Murray, M. Jain, K. J. Thomsen, N. Mercier, How confident are we in the chronology of the transition between Howieson's Poort and Still Bay? *J. Hum. Evol.* **64**, 314–317 (2013).
25. Z. Jacobs, R. G. Roberts, Single-grain OSL chronologies for the Still Bay and Howieson's Poort industries and the transition between them: Further analyses and statistical modelling. *J. Hum. Evol.* **107**, 1–13 (2017).
26. H. Valladas, J. L. Reyss, J. L. Joron, G. Valladas, O. Bar-Yosef, B. Vandermeersch, Thermoluminescence dating of Mousterian Troto-Cro-Magnon' remains from Israel. *Nature* **331**, 614–616 (1988).
27. D. E. Bar-Yosef Mayer, B. Vandermeersch, O. Bar-Yosef, Shells and ochre in Middle Paleolithic Qafzeh Cave, Israel: Indications for modern behavior. *J. Hum. Evol.* **56**, 307–314 (2009).
28. E. Hovers, S. Ilani, O. Bar-Yosef, B. Vandermeersch, An early case of color symbolism: Ochre use by modern humans in Qafzeh Cave. *Curr. Anthropol.* **44**, 491–522 (2003).
29. D. L. Hoffmann, C. D. Standish, M. García-Díez, P. B. Pettitt, J. A. Milton, J. Zilhão, J. J. Alcolea-González, P. Cantalejo-Duarte, H. Collado, R. de Balbín, M. Lorblanchet, J. Ramos-Muñoz, G.-Ch. Weniger, A. W. G. Pike, U-Th dating of carbonate crusts reveals Neanderthal origin of Iberian cave art. *Science* **359**, 912–915 (2018).
30. I. Martínez, M. Rosa, R. Quam, P. Jarabo, C. Lorenzo, A. Bonmatí, A. Gómez-Olivencia, A. Gracia, J. L. Arsuaga, Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain. *Quat. Int.* **295**, 94–101 (2013).
31. D. L. Hoffmann, A. W. G. Pike, M. García-Díez, P. B. Pettitt, J. Zilhão, Methods for U-series dating of CaCO_3 crusts associated with Palaeolithic cave art and application to Iberian sites. *Quat. Geochronol.* **36**, 104–119 (2016).

32. D. L. Hoffmann, J. Prytulak, D. A. Richards, T. Elliott, C. D. Coath, P. L. Smart, D. Scholz, Procedures for accurate U and Th isotope measurements by high precision MC-ICPMS. *Int. J. Mass Spectrom.* **264**, 97–109 (2007).
33. R. Montes, *El Paleolítico Medio en la costa de Murcia* (University of Murcia, 1987).
34. A. H. Jaffey, K. F. Flynn, L. E. Glendenin, W. C. Bentley, A. M. Essling, Precision measurement of half-lives and specific activities of ^{235}U and ^{238}U . *Phys. Rev. C* **4**, 1889–1906 (1971).
35. H. Cheng, R. L. Edwards, J. Hoff, C. D. Gallup, D. A. Richards, Y. Asmerom, The half-lives of uranium-234 and thorium-230. *Chem. Geol.* **169**, 17–33 (2000).
36. N. E. Holden, Total half-lives for selected nuclides. *Pure Appl. Chem.* **62**, 941–958 (1990).
37. K. R. Ludwig, D. M. Titterton, Calculation of $^{230}\text{Th}/\text{U}$ isochrons, ages and errors. *Geochim. Cosmochim. Acta* **58**, 5031–5042 (1994).
38. K. H. Wedepohl, The composition of the continental crust. *Geochim. Cosmochim. Acta* **59**, 1217–1232 (1995).

Acknowledgments: We thank the government of Murcia for sampling permission. We are grateful to I. Martín-Lerma for fieldwork support and to R. Montes for access and permission to use the field documentation from his 1985 excavation of Cueva de los Aviones. **Funding:**

This research was financially supported by the Max Planck Society. **Author contributions:** D.L.H. and J. Zilhão designed the study and wrote the initial manuscript. D.L.H., J. Zilhão, and J. Zapata carried out the fieldwork for sampling flowstone sections in Cueva de los Aviones. D.L.H. performed U-series analyses and data evaluation. All authors contributed to data interpretation and the final manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 17 November 2017

Accepted 16 January 2018

Published 22 February 2018

10.1126/sciadv.aar5255

Citation: D. L. Hoffmann, D. E. Angelucci, V. Villaverde, J. Zapata, J. Zilhão, Symbolic use of marine shells and mineral pigments by Iberian Neandertals 115,000 years ago. *Sci. Adv.* **4**, eaar5255 (2018).

Symbolic use of marine shells and mineral pigments by Iberian Neandertals 115,000 years ago

Dirk L. Hoffmann, Diego E. Angelucci, Valentín Villaverde, Josefina Zapata and João Zilhão

Sci Adv 4 (2), eaar5255.
DOI: 10.1126/sciadv.aar5255

ARTICLE TOOLS

<http://advances.sciencemag.org/content/4/2/eaar5255>

SUPPLEMENTARY MATERIALS

<http://advances.sciencemag.org/content/suppl/2018/02/16/4.2.eaar5255.DC1>

RELATED CONTENT

<http://science.sciencemag.org/content/sci/359/6378/912.full>

REFERENCES

This article cites 32 articles, 10 of which you can access for free
<http://advances.sciencemag.org/content/4/2/eaar5255#BIBL>

PERMISSIONS

<http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)

Science Advances (ISSN 2375-2548) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. 2017 © The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. The title *Science Advances* is a registered trademark of AAAS.